Article

Current Biology

The phylogenetic origin of turtles

Highlights

- New phylogeny reframes the ecological origins of the turtle shell
- Turtles are close relatives of archosaurs, supported by sweeping anatomical evidence
- Largest morphological phylogeny rejects *Eunotosaurus* as a stem turtle
- Turtle-like features in millerettids reflect convergent fossorial adaptation

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In brief

Jenkins et al. present the largest morphological dataset for early reptile phylogeny, recovering turtles as sisters to archosaurs and rejecting *Eunotosaurus* as a stem turtle. Instead, *Eunotosaurus* is a millerettid stem reptile whose turtle-like features arose through convergence, possibly driven by shared fossorial ecology, thus reframing the origins of the turtle shell.

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The phylogenetic origin of turtles

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SUMMARY

The evolutionary origins of turtles remain poorly understood. Molecular systematics posit a sister relationship between turtles and archosaurs, but morphological studies return conflicting hypotheses of turtle relationships both to other living reptiles and to their closest fossil relatives. The middle Permian *Eunotosaurus africanus* has been widely regarded as the oldest stem turtle, which makes it instrumental in recent discussions of the origins of turtles and their highly transformed anatomy. Here, we use anatomical observations derived from X-ray computed microtomography (μCT) of *Eunotosaurus* and candidate stem turtles to evaluate phylogenetic hypotheses of turtle origins. *Eunotosaurus* has many plesiomorphies and lacks synapomorphies of crown reptiles, whereas *Proganochelys*, one of the oldest uncontentious stem turtles, shares similarities with archosauromorphs, especially in the endocranium. Our comprehensive phylogenetic analysis recovers *Eunotosaurus* as a millerettid stem reptile not related to turtles. This indicates that features shared by *Eunotosaurus* and turtles, notably including broadened dorsal ribs, evolved independently. These similarities are better explained by convergent evolution of fossorial ecologies rather than shared ancestry. Furthermore, we find strong support for the molecular phylogenetic hypothesis that turtles are sister to Archosauria among living reptiles, resolving long-standing conflicts between morphological and molecular datasets. By placing turtle origins among the earliest archosauromorphs in the late Permian, we provide new insights into the anatomical transformations involved in the origins of the distinct turtle body plan.

INTRODUCTION

The origin of turtles is a long-standing controversy in vertebrate evolution. Three decades of molecular evidence has provided increasing levels of confidence that archosaurs (birds + crocodylians) are the living sister taxon of turtles, using proteomic,[1–4] karyotypic,[5] and genetic sequences, including mRNA,[6,7] miRNA,[8,9] mitochondrial,[10,11] and nuclear DNA.[12,13] Whereas early anatomical studies identified numerous soft tissue features that are consistent with this hypothesis,[14–20] other morphological phylogenetic studies using evidence from both living and fossil species have instead generally placed turtles as the sister to all other living reptiles (Lepidosauria + Archosauria).

Turtles display a combination of highly modified postcranial anatomy and superficially primitive cranial anatomy that has confounded attempts to identify their Paleozoic fossil relatives. This impedes the understanding of the evolutionary origins of turtles and their distinctive body plan. Several Paleozoic reptile groups have been proposed by paleontologists as stem turtles, including Carboniferous "anapsids"[21–29] such as the Captorhinidae,[16,26,27] Permian "parareptiles"[30,31] such as Procolophonidae[32] and Pareiasauria,[30,31,33] and the Sauropterygia, a large radiation of Mesozoic marine reptiles with enigmatic phylogenetic affinities.[34–39] These different hypotheses characterize turtles as either primitive amniotes or anapsids due to the lack of temporal fenestration,[21–25,40] or as "diapsids" that have secondarily closed their temporal fenestrae.[40–45]

Until recently, the earliest known unambiguous stem turtle was *Proganochelys quenstedtii* from the Late Triassic of Germany, which already shows an anapsid skull and the fully formed carapace and plastron[46] characteristic of turtles. The last two decades have revealed several more stem turtles with plesiomorphic and intermediate morphologies documenting the closure of the temporal fenestrae and the evolution of the turtle shell.[36–38,47] Most of these recent studies consider the middle Permian taxon *Eunotosaurus* to be the oldest stem

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turtle,[35–37,41,42,44,48–50] (but see Simões et al.,[51] Gow,[52] Cox,[53] and Cisneros et al.[54]), which makes this South African taxon central to the hypotheses of turtle origins.[48,55–58]

If *Eunotosaurus* is indeed the oldest stem turtle, it would also be the earliest known crown reptile (predating other crown reptiles by ~10 Ma) and providing strong implications for molecular divergence estimates.[13] Yet, *Eunotosaurus* has conspicuous plesiomorphies that would place turtles outside the lepidosaur-archosaur split[35,42,51] or closer to lepidosaurs than to archosaurs,[35,36] which stands in stark contrast to the strong molecular support for a turtle-archosaur relationship (Archelosauria).[1–13] Character evidence linking *Eunotosaurus* to turtles, such as its broadened, T-shaped dorsal ribs and the inferred closure of an upper temporal fenestra,[35,42] is also shared with millerettid stem reptiles,[25,52] calling into question their exclusivity as diagnostic characters of turtle origins. These incongruences, together with recent advances in early reptile systematics[59–67] and morphological character systems, underscore the need for an integrative anatomical and phylogenetic study that evaluates the affinities of *Eunotosaurus* alongside other hypothesized stem turtles. Here, we use anatomical observations derived from X-ray computed microtomography (μCT) of *Eunotosaurus* and candidate stem turtles to provide that evaluation. We find strong evidence that *Eunotosaurus* is a millerettid stem reptile, which allows us to infer that striking anatomical similarities between millerettids and turtles—including broadened, overlapping ribs and a shortened trunk—are convergences likely driven by shared fossorial ecologies. We also find strong support for an archosaur-turtle relationship from morphological data, resolving long-standing conflicts between morphological and molecular hypotheses of turtle origins.

RESULTS

Anatomical support for *Eunotosaurus* as a millerettid stem reptile

We conducted a comprehensive revision of *Eunotosaurus*, in which we studied all available specimens by both physically examining specimens and by μCT (Figures 1–3 and S1–S3). The uncrushed skulls of recently discovered *Eunotosaurus* (e.g., BP/1/7852 and BP/1/8010) show that earlier reconstructions based on the poorly preserved, taphonomically distorted skull of CM-777 (resegmented here, Figure S1) are inaccurate, which presents an opportunity to reassess proposed homologies between *Eunotosaurus*, millerettid stem reptiles, and turtles.

The skull roof of *Eunotosaurus* is covered by cranial osteoderms and the external nares are expanded—features that are uniquely shared with millerettid stem reptiles.[60,69,70] Scans of CM-777 reveal that the tooth roots show plicidentine grooves, a plesiomorphy that is absent in crown group reptiles. The posterior skull bears paired postparietals, supratemporals, and tabulars (Figure S1), with the latter being absent in all known crown reptiles including turtles.[46] Bever et al.[35] proposed that *Eunotosaurus* juveniles possessed an upper temporal fenestra that was then closed by growth of a "supratemporal" through ontogeny, implying a neodiapsid ancestry. Our segmentation shows that this element is instead a misidentified ventral flange of the parietal (Figure 1), which is consistent with earlier observations.[52] Ontogenetic closure of an upper temporal fenestra, or gap, through the growth of the parietal, also occurs in millerettids but not in any other taxa to our knowledge. The parietal of *Eunotosaurus* lacks any lateral embayment on the ventral surface for the jaw adductor musculature, which is in contrast to early neodiapsids, crown reptiles, and uncontroversial stem turtles such as *Proganochelys* and *Kayentachelys*.[71]

The palate of *Eunotosaurus* bears plesiomorphic features that contrast with turtles and other crown reptiles. The vomers are paired and bear enlarged anterior teeth, which is a unique synapomorphy of millerettids among Paleozoic stem reptiles.[72] The palatines carry a small field of 2–3 tooth rows, the ectopterygoid is edentulous, and the pterygoid retains a field of teeth on the transverse flange and two fields on the palatal ramus. The interpterygoid vacuity is narrow, and the rounded contours reconstructed for CM-777 reflect preparation damage, which is best shown by the undamaged pterygoid of CGP/1/3000. The suborbital fenestra is absent, unlike neodiapsids including stem turtles such as *Pappochelys*.[36] Striking plesiomorphies of the *Eunotosaurus* braincase refute a position in the reptile crown group, or even within Neodiapsida. For example, the parabasisphenoid bears teeth on both the cultriform process and on the ventral plate (where it is organized into two rows), as in millerettids, and posteriorly the ventral plate of the parabasisphenoid remains flat, lacking the pharyngeal recess seen in neodiapsids.[61] The prootic lacks the anterior inferior process and crista prootica, which are key synapomorphies of crown reptiles that we identify here in the stem turtle *Proganochelys quenstedtii* (Figure 2). In the region of the crista prootica of crown reptiles, a low ridge is present in *Eunotosaurus*, which is similar to crownward stem reptiles including millerettids and neodiapsids.[60,61] *Eunotosaurus* has no laterosphenoid, which is different from many archosauromorphs and the stem turtle *Proganochelys* (Figure 2). The thin element identified in the orbit of *Eunotosaurus*, identified as a laterosphenoid by Bever et al.,[35] is a scleral ossicle. The quadrate bears a large stapedial boss on the medial surface, which is absent in crown reptiles.[60] There is no prootic-quadrate, and so this feature cannot be used to support a *Eunotosaurus*-turtle relationship (contra, see Bever et al.[35]) (Figure S1). The stapes is robust, with a large stapedial foramen and a distal end that is broader than the footplate (Figure 3). These traits are present in *Milleretta*[69] (Figure 3) and other stem reptiles, whereas the stapedial foramen is absent in both stem turtles and stem archosaurs.[46] These observations are corroborated by a recent study on the inner ear of *Eunotosaurus*, which noted numerous similarities with stem reptiles to the exclusion of archosauromorphs and turtles.[73]

The postcranium of *Eunotosaurus* preserves a mosaic of primitive and apomorphic features. There are six cervical vertebrae, as in *Milleretta*,[72] whereas stem turtles and other archosauromorphs bear eight or more cervicals.[74] Nine elongate dorsal vertebrae are present—11 fewer than most stem and crown reptiles,[16] six fewer than in *Milleretta*, three fewer than the stem turtle *Eorhynchochelys*,[37] and one fewer than Testudinata.[41,42] The dorsal ribs expand through ontogeny, with large gaps between ribs in juvenile or subadult individuals (BP/1/8010) and distal overlap as in *Milleretta* (Figure S2), contrasting with the broad but non-overlapping ribs of early non-shelled stem turtles.[37,38,47] This rib expansion leads to a T-shaped cross section, which is

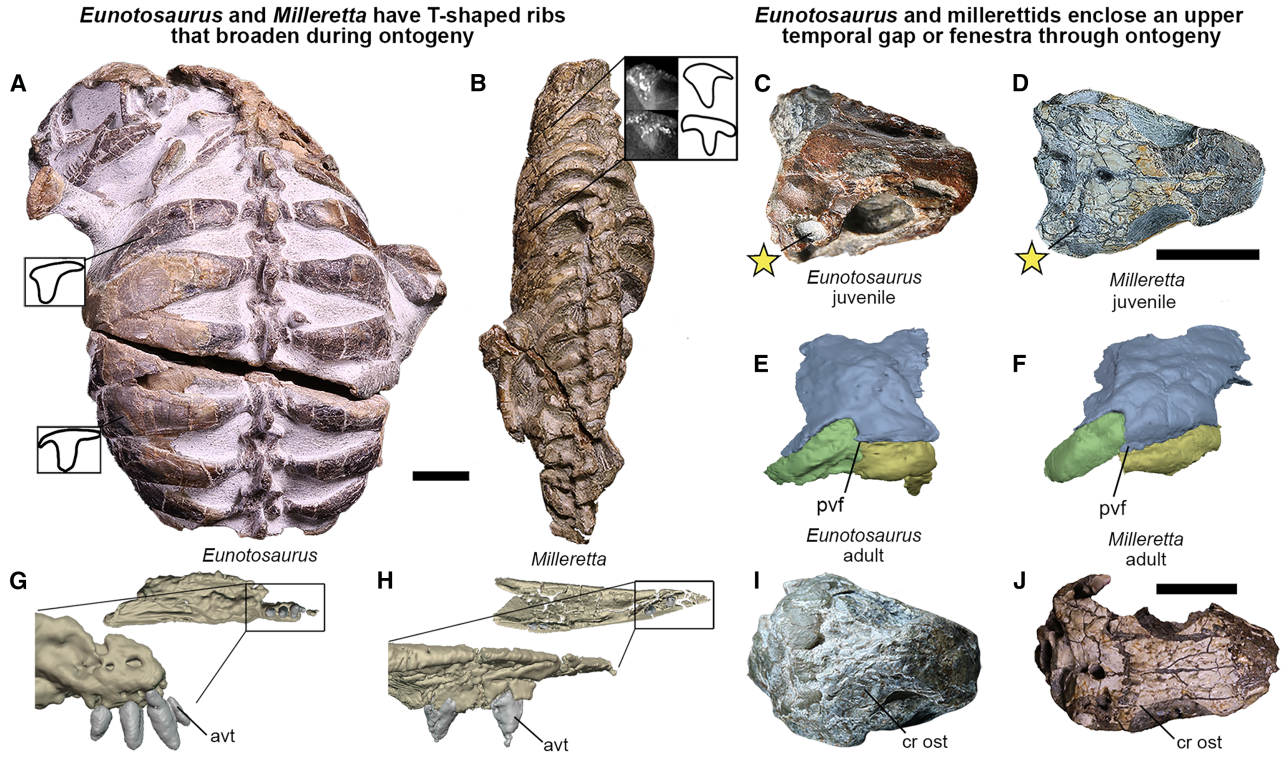

Figure 1. Skeletal anatomy of *Eunotosaurus africanus* compared with the millerettid stem reptile *Milleretta rubidgei*, emphasizing millerettid synapomorphies and shared ontogenetic trends in both taxa

(A) Referred specimen BP/1/7852 of *E. africanus* in dorsal view.

(B) Adult individual of *M. rubidgei* (BP/1/2040), with cross sections of the eight dorsal rib demonstrating the T-shaped rib morphology characteristic of this taxon (also see Figure S2).

(C and D) Skulls of juvenile individuals of (C) *E. africanus* (SAM-PK-K790) and (D) *M. rubidgei* (SAM-PK-7366) in dorsal view.

(E and F) Right parietal, postorbital, and supratemporal of (E) adult *E. africanus* specimen (CM-777) and (F) *M. rubidgei* (BP-1-3010), showing the presence of a ventral parietal flange (pvf) enclosing the upper temporal fenestra.

(G and H) Vomers in ventral and lateral view showing the presence of enlarged anterior vomerine teeth (avt) in *E. africanus* (CM-777) and *M. rubidgei* (BP-1-3822).

(I and J) Skulls of adult individuals of *E. africanus* (SAM-PK-K1135) and *M. rubidgei* showing the closure of the upper temporal gap and the diagnostic cranial osteoderms (cr ost) of Millerettidae. Scale bars, 1 cm.

See also Figures S1 and S2.

similar to some stem turtles[41,42] that we also identify in *Milleretta* (Figures 1 and S2). The neural arches of the dorsal centra are convex dorsally and lack the zygapophyseal laminae present in early turtles and archosauromorphs.[59,75] The gastralia comprise a single lateral element per centrum, as in *Milleretta*, but differ in bearing a facet for a cartilaginous sternal rib on the lateral ends.[47]

The scapula lacks an acromion process unlike in stem and crown turtles.[76] The humerus is long and slender and lacks an expanded proximal end, and it bears both entepicondylar and ectepicondylar foramina, the former being absent in stem turtles and stem archosaurs.[55,74] The pelvic anatomy of BP/1/6218 and GCP/1/3000 reveals a pubis lacking the lateral pubic process, epipubic process, and midline keel, unlike in stem turtles and pareiasaurs.[77,78] The femur is straight as in millerettid stem reptiles, differing from the sigmoidal femur of neodiapsids including stem turtles.[59] The astragalus and calcaneum (preserved in AM 5999 and FPM 2014.269) are unfused and a complete series of five distal tarsals with an unhooked metatarsal V, as in stem reptiles (Figure 3). This is in stark contrast to the hooked fifth metatarsal of turtles and other crown reptiles, which is formed by the fusion of the fifth distal tarsal and fifth metatarsal during development.[36,46,74]

New information on the oldest unambiguous stem turtles

CT data for two unambiguous stem turtles, *Proganochelys quenstedti* (Late Triassic) and *Kayentachelys aprix* (Early Jurassic) expose previously undetected archosauromorph synapomorphies, which are shared with stem archosaurs such as *Prolacerta broomi* (Figures 2 and 3).

The earliest stem turtles such as *Pappochelys* were anatomically diapsid,[36] and our μCT observations show that the braincase of *Proganochelys* has a suite of crown-reptile features that are absent in *Eunotosaurus*. These include an anterior inferior process of the prootic, a crista prootica, and an enlarged metotic foramen (Figures 2 and 3). The presence of a laterosphenoid framing an open epioptic fenestra in *Proganochelys* (Figure 2) is shared with early stem archosaurs.[66] *Proganochelys* retains

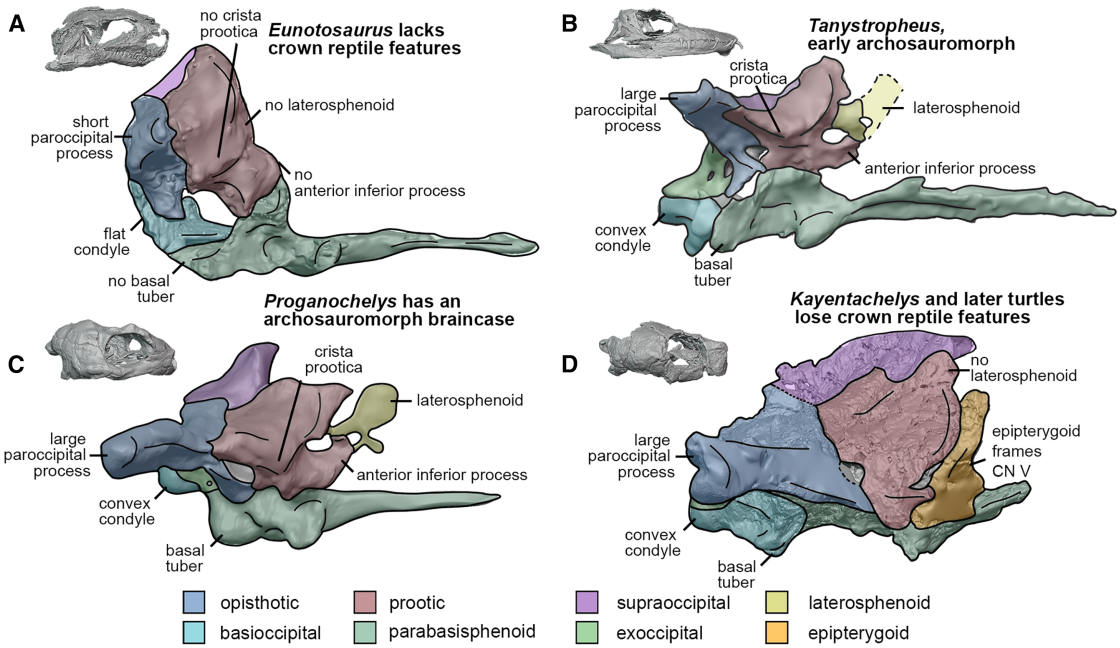

Figure 2. Comparative braincase morphology in early reptiles and stem turtles based on tomographic data

(A) *Eunotosaurus africanus* (CM-777).

(B) Archosauromorph *Tanystropheus hydroides* (PIMUZ T 279095).[68]

(C) Stem turtle *Proganochelys quenstedti* (SMNS 16980), with laterosphenoid reconstructed based on SMNS 15759.

(D) Jurassic stem turtle *Kayentachelys aprix* (TMM 43670–2).

these plesiomorphies from a turtle-archosaur ancestor, whereas more crownward turtles have strongly modified cranial architecture related to the evolution of neck retraction and adductor muscle redirection over an enlarged otic capsule,[79,80] overprinting these ancestrally archelosaurian features (Figure 2). The modified braincase features of more crownward stem turtles such as *Kayentachelys* include an enclosed cranioquadrate space formed by a fused prootic-quadrate-pterygoid region around the canalis cavernosus[76,79] and replacement of the anterior inferior process of the prootic by the epipterygoid to frame the trigeminal foramen (CN V)[57] (Figures 2, 3, and S1B). This foramen later becomes incorporated into a secondary lateral braincase wall formed by a neomorphic pterygoid-parietal contact, which is crownward of *Kayentachelys*.[56,81] These cranial transformations entail substantial reorganization of the temporal region, with the adductor musculature inserting on the lateral wall of the braincase, forcing topological changes in the anatomy of soft tissues such as the internal carotid arteries and cranial nerves.[71,82] This reorganization of posterior cranial anatomy has undoubtedly contributed to uncertainty over the evolutionary relationships of turtles within Reptilia.

Phylogenetic results

Phylogenetic analyses were conducted using a modified and substantially expanded version of the dataset of Jenkins et al.,[60,61] designed to test all major hypotheses of turtle origins by incorporating all fossil reptile groups implicated in turtle origins together with the anatomical observations and character evidence originally advanced in support of each of these hypotheses[27–42,47,83] (see STAR Methods).

Phylogenetic analysis firmly recovers *Eunotosaurus* as a millerettid stem reptile, far removed from turtles and other crown reptiles (Figures 4, S3, and S4). *Eunotosaurus* emerges as sister to the late Permian *Milleretta rubidgei* (posterior probability = 1), which shares many of its turtle-like traits.[52,54] Twelve unambiguous synapomorphies diagnose this sister relationship, including the parietal closure of an unossified gap in the temporal region during ontogeny, and the presence of overlapping dorsal ribs with T-shaped cross sections (Figure S5). An additional 31 unite *Eunotosaurus* with Millerettidae (e.g., the presence of cranial osteoderms and enlarged anterior vomerine teeth; Figures 3 and S5). Millerettids, including *Eunotosaurus*, retain numerous plesiomorphies that are absent in crown reptiles including turtles, such as the presence of tabulars, postparietals, a stapedial foramen, and a distinct fifth distal tarsal. They lack crown-reptile synapomorphies such as a cephalic condyle of the quadrate and a hooked fifth metatarsal (Figures 2 and 3).

We find strong morphological support for an archosaur-turtle relationship in our analyses (Figure 4). Bayesian analysis returns turtles as one of the earliest-diverging archosauromorph clades, sister to Tanystropheidae + Crocopoda. Archelosauria (posterior probability = 0.88, bracketed by unambiguous support values of 1; Figure S3) is supported by at least 25 synapomorphies, including a small laterosphenoid framing a fenestra epioptica, an inferior parietal process[46] embayed by the adductor musculature and articulating with the braincase, and parallelogram-shaped cervical vertebrae with postzygapophyseal laminae (Figure S5). An additional 47 synapomorphies provide robust support for the inclusion of turtles within Archosauromorpha (posterior probability = 1; Figure S3), which is consistent with

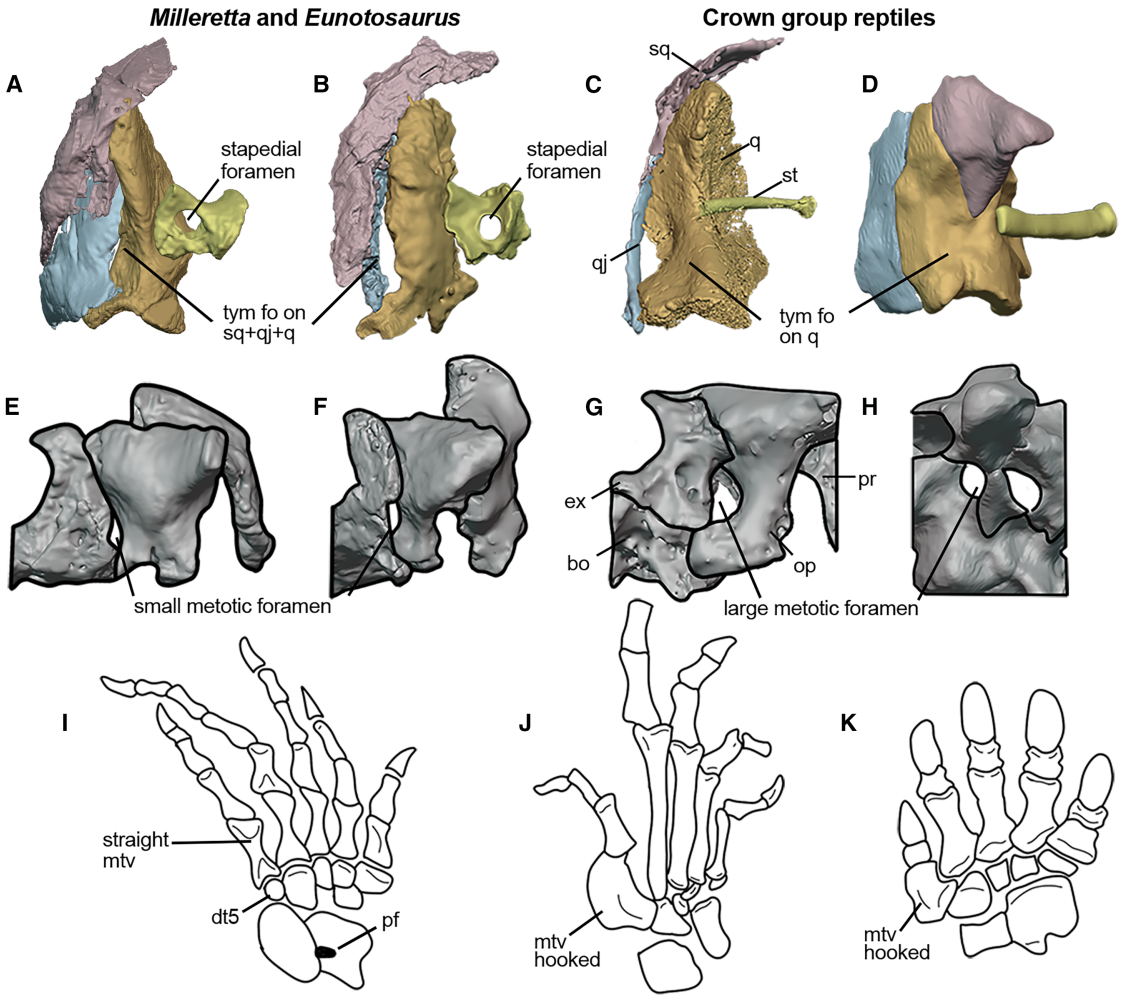

Figure 3. Tympanic, otooccipital, and pedal anatomy of millerettids and crown reptiles

(A–D) Tympanic region illustrating a squamosal-dominated tympanic fossa in (A) *M. rubidgei* (BP/1/3822) and (B) *E. africanus* (CM-777), which contrasts with a quadrate-dominated tympanic fossa in (C) *Prolacerta broomi* (BP/1/5880) and (D) *P. quenstedti* (SMNS 16980).

(E–H) Occipital region (same specimens) of (E) *M. rubidgei*, (F) *E. africanus*, (G) *P. broomi*, and (H) *P. quenstedti*, which highlights the differences in the morphology of the meiotic foramen between stem and crown reptiles.

(I–K) Pes of (I) *E. africanus* (AM 5999), (J) *P. broomi* (AMNH 9502), and (K) *P. quenstedti* (SMNS 17204, SMNS 16980), which illustrates the absence of crown-reptile pedal specializations in *E. africanus*.

Abbreviations: bo, basioccipital; dt5, distal tarsal 5; ex, exoccipital; mtv, fifth metatarsal; op, opisthotic; pf, perforating foramen; pr, prootic; q, quadrate; qj, quadratojugal; sq, squamosal, st, stapes.

high rates of morphological evolution among early archosauromorphs[74,84,85] and suggests that stem turtles first originated during the deep diversification of archosauromorphs immediately preceding the end-Permian mass extinction (Figure S3).

Our constraint analyses show that alternative hypotheses for the placement of Pantestudines (total-group turtles) require substantially longer trees. Hypotheses of turtle origins from Captorhinidae (+153 steps; $p < 0.001$), Procolophonidae (+109 steps; $p < 0.001$), or Pareiasauria (+92 steps; $p < 0.001$) are rejected (Figure S6). Placement of *Eunotosaurus* as a stem turtle is similarly disfavored (+93 steps; $p < 0.001$) and requires millerettids to be included within the turtle stem, in contrast to previous analyses recovering a *Eunotosaurus*-turtle clade that is unrelated to other millerettids.[35] Alternative hypotheses placing turtles within Lepidosauromorpha are also rejected (+27 steps; $p = 0.0046$). By contrast, a sister-group relationship between Pantestudines and Sauropterygia within Archosauromorpha cannot be statistically rejected, although this topology remains longer than the unconstrained trees (+16 steps; $p = 0.1315$) (Figure S6). Collectively, these results indicate that non-archosauromorph hypotheses for turtle origins are poorly supported by morphology.

DISCUSSION

Closing the morphology-molecule divide in turtle origins

Early comparative and developmental studies of skeletal anatomy struggled to identify the relationships of turtles to other

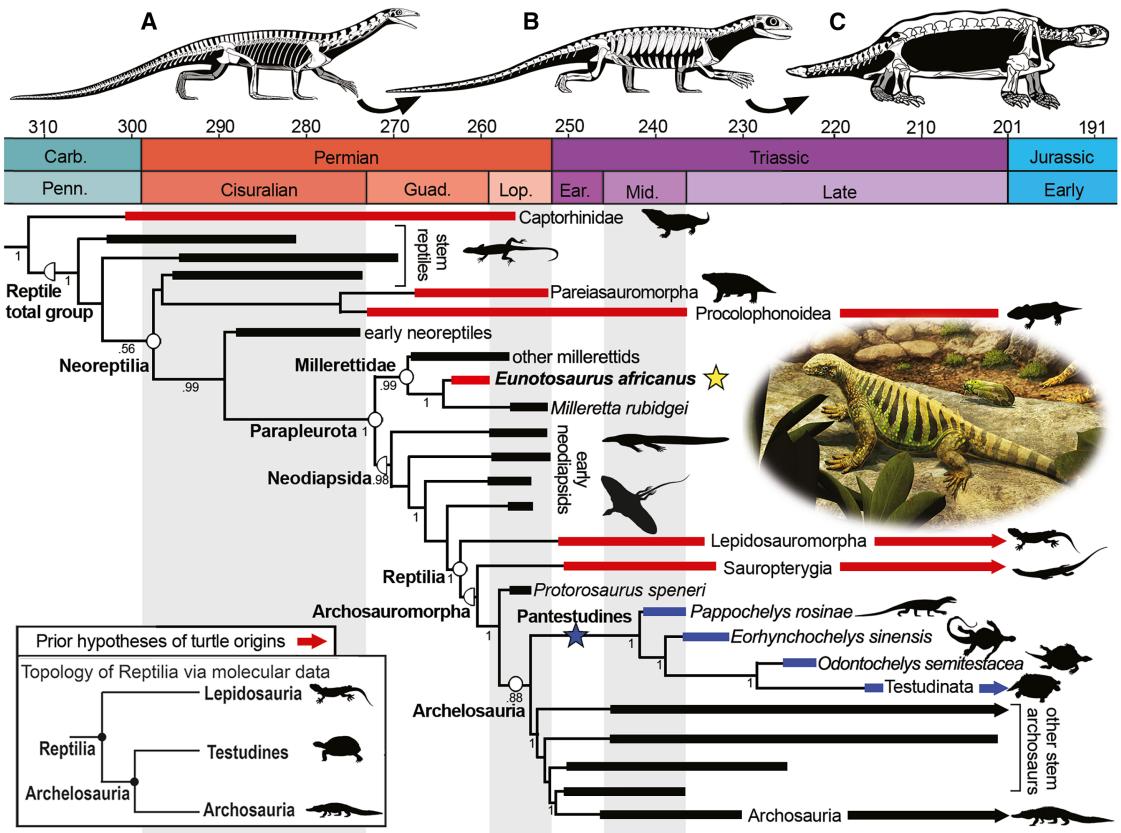

Figure 4. Simplified cladogram of early reptiles showing the placement of *E. africanus* and stem turtles

(A–C) Red occurrence lines indicate taxa previously proposed as stem turtles; blue lines denote unambiguous stem turtles. The placement of Sauropterygia within Archosauromorpha follows our parsimony analysis, although they are found as lepidosauromorphs in the Bayesian analysis. Posterior probabilities > 0.50 are labeled below nodes (also see Figure S3). Skeletal reconstructions of (A) *Protorosaurus speneri*, (B) *Pappochelys rosinae*, and (C) *Proganochelys quenstedti* depict the hypothesized evolutionary transition from a protorosaur-like ancestor to early turtles. Skeletal reconstruction of *P. speneri* and *P. rosinae* by LiterallyMiguel, and *P. quenstedti* derived from Gaffney.[46] Silhouettes are available from Phylopic (www.phylopic.org) under CC BY 3.0 licenses or within public domain.

See also Figures S3–S5.

reptiles due to uncertainty regarding homologies in the temporal region of the skull, and of the elements comprising the shell.[21,50,86–89] The general consensus of this earlier work was that turtles were primitive amniotes or anapsids due to the lack of temporal fenestration[21–25] or that turtles were diapsids that secondarily closed their temporal fenestrae.[90,91] However, numerous soft tissue features have been recognized as consistently uniting turtles with archosaurs, including the absence of a Jacobson's organ in the nasal capsule,[14] the attachment of the nictating membrane to the pyramidalis muscle in the eyelid,[15–17] the innervation of the jaw adductor musculature by the trigeminal nerve,[19] and the presence of the secondary subclavian artery of the heart.[18,20] Proteomic work has corroborated this placement, with turtles sharing numerous proteins, such as beta-keratins, that are more similar to those of archosaurs.[3] Over the past three decades, as the diversity and sophistication of molecular analyses have increased, support for a placement of turtles as sister to Archosauria[1–13] has only strengthened. The morphological support for Archelosauria recovered here demonstrates that the long-standing conflicts between molecular and morphological datasets was not a genuine signal of discordance, but rather a data gap in skeletal morphology now closed by a rapidly improving fossil record and new imaging techniques.

Anatomical transformations in the origin of the turtle body plan

The removal of *Eunotosaurus* from the turtle stem, and the placement of Pantestudines within Archosauromopha, invites a reconsideration of the ancestral turtle body plan and clarifies the sequence of trait evolution during turtle origins and for crown reptiles more broadly. For instance, the hooked fifth metatarsal,[62] quadrate-supported tympanic fossa, and slender stapes, which were previously interpreted to be convergently acquired in turtles in part due to their absence in *Eunotosaurus*,[92] are in fact synapomorphies of crown reptiles (Figure 3). Beyond these reptile-wide implications, the new position of *Eunotosaurus* also clarifies the sequence of postcranial transformations along the turtle stem itself.

A turtle placement near the base of Archosauromorpha suggests that the earliest stem turtles would have been "protorosaurian" or *Prolacerta*-like in structure, as they were small

bodied but bore a suite of archosauromorph features. In the cervical series and pelvic girdle, such features are indeed retained in *Pappochelys*[48] and *Eorhynchochelys*,[37] including an elongated neck formed by laminated cervical vertebrae and a postacetabular process of the ilium bearing well-developed striae for *M. iliotibialis*. The loss of these features in the postcranium is part of the drastic reorganization of the entire body plan in more derived stem turtles (Figure 2), and it includes not only well-recognized features relating to the formation of the carapace[86,87,93–95] but also a restructuring of their fore- and hindlimbs for fossorial and aquatic ecologies.[82] Other postcranial changes (e.g., changes in femur morphology that correspond strongly to the form of the humerus in testudinatans) postdate the origin of the shell, as there is evidence that the shell constrains these postcranial features of testudinatans by enforcing specific proportions between carapace length and humerus and femur lengths[55] or by limiting humerus disparity patterns.[11,96] Some major changes in the cranium (e.g., ectopterygoid and postfrontal loss; retained in *Pappochelys*) must occur during early stem turtle evolution before the acquisition of the shell,[81] whereas other changes (e.g., direct connection of the palate and skull roof via a pterygoid-parietal contact or epipterygoid, Figure 2; fusion of basicranial joints; and enlargement of otic capsule with redirection of adductor musculature)[55,71,81] occurred after the origin of the shell. Positioning *Eunotosaurus* among millerettids removes much of the morphological uncertainty about the evolution of these features, providing clarity on how stem turtles evolved from a generalized archosauromorph ancestor in the late Permian to become a well-established and morphologically specialized group by the Middle Triassic.

Convergent evolution of fossorial reptiles and the origins of the turtle shell

Fossoriality has been repeatedly implicated in the early evolution of the turtle body plan, particularly under hypotheses that *Eunotosaurus*[41,42,44,47,57,58,97,98] is a stem turtle. Our phylogenetic findings instead suggest that features shared by millerettids and turtles result from convergent evolution including a short trunk (<12 dorsal vertebrae) and broad, overlapping ribs. *Eunotosaurus* as an anatomically derived millerettid and therefore represents a striking evolutionary replicate of "turtleization" among stem reptiles prior to and independent of turtle origins. Millerettids, including *Eunotosaurus*, display numerous fossorial adaptations that have been linked to scratch-digging with trunk and neck stabilization in turtles (e.g., reinforced cervical vertebrae, reduced vertebral column, broad ribs, and enlarged manual unguals),[41,42,58] which is a functional interpretation supported by their association with burrow structures across the Karoo Basin.[25,99,100] The fossorial ecology inferred for millerettids may have been the ecological driver for the broadened ribs of these taxa, although overlapping ribs also occur in other extinct reptile groups such as terrestrial pareiasaurs and semiaquatic cyamodontid and saurosphargid sauropterygians. The latter two groups independently evolved a superficially turtle-like shell composed entirely of dermal osteoderms, standing in contrast to the intermembraneous plastron and mixed dermal-endochondral carapace of true turtles.[101,102]

The plausible fossorial and terrestrial habits of *Eunotosaurus*, now divorced from the turtle stem lineage, invite reconsideration of past hypotheses for a strictly fossorial origin of the turtle shell. The earliest known Triassic stem turtles—each lacking a fully formed carapace—are associated with aquatic sediments: *Pappochelys* is linked to freshwater environments[36] and *Eorhynchochelys* and *Odontochelys* are known from shallow marine strata.[37,38] Histological evidence from *Pappochelys*, while previously interpreted as supporting fossoriality—an interpretation shaped in part by prior observations of *Eunotosaurus*—was itself acknowledged by that same study to be equally compatible with an amphibious ecology.[97] Similarly, *Odontochelys*, the first stem turtle to show a complete plastron, is hypothesized to have been at least semiaquatic based on histological and isotopic evidence,[103,104] and to have used its plastron as a ballast while swimming, yet it too retains enlarged claws. In fact, many semiaquatic reptiles and mammals today excavate burrows for nesting or thermoregulation,[105,106] which is consistent with the retention of enlarged claws in stem turtles—something conspicuously absent in fully aquatic sauropterygians[62]—and the prevalence of buried nests and burrowing behavior in extant turtles. The evolution of the integrated turtle shell, which comprises a rib-dominated carapace and complete plastron, thus plausibly reflects a combination of selective regimes: the thickened ribs inherited from a fossorial ancestor were subsequently co-opted for aquatic adaptation as the earliest stem turtles colonized freshwater and marine environments.

The late Permian origin of Archelosauria

By recovering turtles as archosauromorphs, our results help clarify the origin of crown group Reptilia. The finding of *Eunotosaurus* (265 Ma) outside the crown group reconciles paleontological evidence of early reptile evolution with molecular clock analyses that estimate the origin of crown reptiles near 260 Ma and the turtle-archosaur split around 255 Ma[8] (Figure 4). This placement minimizes inferred ghost lineages for Lepidosauromorpha (~15 Ma) and Archosauromorpha (~8 Ma) and supports a late Permian origin for the reptile crown group, which is in concordance with molecular studies. Last, our topology reduces the ghost lineage at the base of Pantestudines by 10 Ma, which now extends from the molecular clock age of Archelosauria (255 Ma) and the occurrence of *Pappochelys* in the Middle Triassic (Ladinian, 240 Ma). It also clarifies that total-group turtles were not survivors of the end-Capitanian mass extinction but rather originated afterward. This suggests that the early diversification of turtles mirrored the cryptic evolutionary radiations of other specialized archosauromorphs such as tanysaurians and rhynchosaurs that likewise developed highly derived anatomies by the Middle Triassic after diverging in the late Permian.[75,84] By embedding turtle origins among other crown-reptile groups, our results help set a new stage for understanding the explosive diversification of Archosauromorpha in the Triassic Period in the wake of the end-Permian mass extinction.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Xavier Jenkins (xjenkins@amnh.org).

Materials availability

This study did not generate any new, unique reagents.

Data and code availability

- The character-taxon data have been deposited at OSF at https://osf.io/t945w and are publicly available as of the date of publication.
- All original code including analytical to conduct the morphological phylogenetic analysis in MrBayes and constraint analyses in PAUP are available at https://osf.io/t945w, which is available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

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AUTHOR CONTRIBUTIONS

Conceptualization, X.A.J., B.R.P., R.B.J., and J.N.C.; data curation, J.N.C. and C.B.; formal analysis, X.A.J. and R.B.J.; investigation, X.A.J., B.R.P.,V.B., G.M., C.M., A.J.F., S.E., R.B.J., and J.N.C.; methodology, X.A.J., V.B., G.M.,C.M., V.F., K.D., and R.B.J.; resources, X.A.J., B.R.P., R.B.J., M.D., C.B., S.E., and J.N.C.; visualization, X.A.J., B.R.P., G.M., C.M., and T.W.G.; writing—original draft, X.A.J., B.R.P., V.B.J.B., R.B.J., S.E., M.D., and J.N.C.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Phylogenetic character matrix (962 characters, 226 OTUs)	This paper	https://osf.io/t945w
Code for conducting Bayesian analysis (FBD tip-dating)	This paper	https://osf.io/t945w
Most parsimonious trees (equal weights and implied weights)	This paper	https://osf.io/t945w
Software and algorithms		
MrBayes v.3.2.7a	Ronquist et al.[107]	https://nbisweden.github.io/MrBayes/
TNT v.1.6	Goloboff and Morales[108]	https://www.lillo.org.ar/phylogeny/tnt/
PAUP* v.4.0a169	Swofford[109]	https://paup.phylosolutions.com/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Please omit this section if your study does not use experimental models typical in the life sciences (e.g., computational or physical science research).

METHOD DETAILS

Phylogenetic dataset

We conducted a phylogenetic analysis to investigate the evolutionary relationships of *Eunotosaurus* and other candidate stem turtles among major Permian and Triassic reptile groups. Our dataset, which extends from previous studies of early amniote and stem reptile morphology,[60,61] is the largest anatomical data matrix to investigate turtle origins to date with 962 characters and 226 OTUs. Our dataset results from a comprehensive evaluation of all anatomical character states used previously in hypotheses of turtle origins,[27,32,34–48,51,52,55,56,59,71,81,83] synthesizing important historical observations,[21–30,32] recent fossil discoveries,[36–38] and new anatomical data from μCT studies of stem-reptile anatomy.[65,66,110] Our analysis greatly improves on other recent datasets of turtle origins by testing the phylogenetic relationships of extinct groups previously hypothesized to be close outgroups to turtles including Captorhinidae, Procolophonidae, Pareiasauria, and Sauropterygia, as well as widely-accepted Triassic and Jurassic stem turtles such as *Pappochelys*, *Odontochelys*, *Eorhynchochelys*, *Proganochelys*, *Proterochersis*, *Paleochersis*, *Kayentachelys*, and *Australochelys*. See Data S1 for the character list.

Computed tomography and segmentation

The PPC-SRμCT data of *Eunotosaurus* specimen CM-777, scanned as part of an earlier study,[35] were processed and segmented using Dragonfly 2024.1 (https://www.theobjects.com/dragonfly/), and regions of interest were exported into Blender 4.2 (https://www.blender.org/) for modelling, reconstruction, and figure creation. The retrodeformed reconstruction provided in Figure S1 is based on careful study of all known *Eunotosaurus* specimens, particularly BP/1/7852, BP/1/8010, and MK 16-1.

QUANTIFICATION AND STATISTICAL ANALYSIS

Bayesian tip-dating inference

Tip-dating phylogenetic inference was conducted in MrBayes 3.2.7a using an Mkv substitution model with a fossilized birth–death (FBD) tree prior. This analysis employed a 'standard' datatype with coding set to 'variable' and rates modeled using a gamma distribution of rate variation among characters. The ages of all operational taxonomic units (OTUs) were assigned uniform distributions, spanning their respective minimum and maximum first occurrence dates. The tree age prior was specified as an offset-exponential distribution (x, y), where x corresponds to the oldest fossil in the dataset, *Whatcheeria deltae* (347.6 Ma), and y represents the earliest estimated divergence of the hypothetical common ancestor, here assumed to be *Tiktaalik* (372 Ma). For each analysis, two independent runs, each with four chains at a temperature of 0.9, were executed for 100 million generations, sampling every 10,000 generations, with the first 50% discarded as burn-in. Convergence was confirmed by a standard deviation of split frequencies <0.01, effective sample sizes greater than 200 for all tested parameters, and an average potential scale reduction factor of 1.01 or less. The posterior probabilities calculated and figured for each node (Figure 4) represent the proportion of post-burn-in trees in which that node was recovered, providing a measure of clade support that incorporates phylogenetic and temporal uncertainty across the sampled parameter space

Maximum parsimony analyses

Maximum parsimony analyses were carried out in TNT v.1.6[108] under equal weights and extended implied weighting. For the latter, a k value of 3 was selected, as lower k values more aggressively downweight homoplastic characters, allowing us to assess the sensitivity of our results to weighting scheme. Tree searches employed a New Technology Search strategy with Sectorial Search, Ratchet, Drift, and Tree Fusing activated. The resulting most parsimonious trees were then subjected to a final round of tree bisection and reconnection (TBR) branch swapping. Bootstrap support values (GC frequencies) were obtained using a traditional search over 1,000 replicates. Bootstrap GC frequencies reflect the percentage of pseudoreplicate trees in which a given clade was recovered across 1,000 replicates, providing a measure of support for each node under the respective weighting scheme (Figure S4). To reconstruct the ACCTRAN/DELTRAN optimizations and corresponding unambiguous synapomorphies for relevant nodes (see Figure S5), we conducted a heuristic search with tree bisection and reconnection, with 1,000 random addition replicates in PAUP* 4.0a169.[109]

Constraint analyses and Templeton tests

We conducted topological constraint analyses under maximum parsimony in PAUP* v.4.0a[109] to evaluate how alternative phylogenetic hypotheses of turtle origins impact tree topology, length, and resolution. An equal-weights parsimony analysis was conducted using a heuristic search with TBR, yielding 96 most parsimonious trees (MPTs; length = 8,245 steps), which served as the baseline for subsequent constraint analyses. Pairwise Templeton tests were used to compare each topologically constrained analysis with the unconstrained MPT. Constraints tested included the placement of Pantestudines within Captorhinomorpha,[26,27] Owenettidae,[32] Pareiasauria,[30,31,33,40,83] and Lepidosauromorpha,[66] as well as a sister-group relationship between Pantestudines and Sauropterygia[34] and the placement of *Eunotosaurus africanus* as sister to Pantestudines (Figure S6). For each pairwise comparison, a Templeton test p-value of $\leq$0.05 was taken as the threshold for rejecting the constrained topology as a significantly worse explanation of the data relative to the unconstrained MPT. Full results including test statistics are provided in Table S1.

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Supplemental Information

The phylogenetic origin of turtles

Xavier A. Jenkins, Brandon R. Peecook, Jonah N. Choiniere, Valentin Buffa, Julien Benoit, Claire Browning, Vincent Fernandez, Kathleen Dollman, Timothy W. Gomes, Gary A. McGaughey, Cy J. Marchant, Adam J. Fitch, Michael O. Day, Serjoscha W. Evers, and Roger B.J. Benson

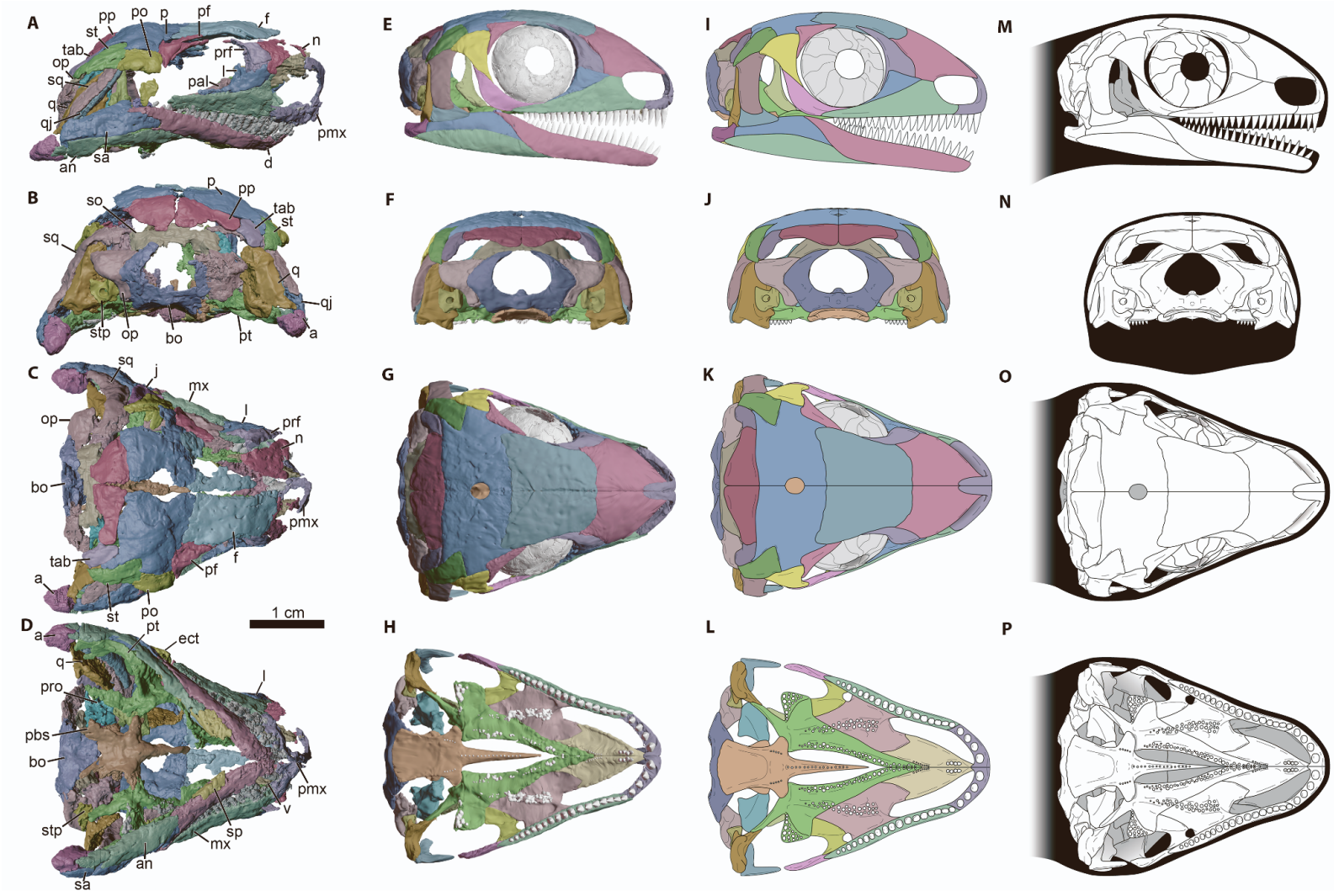

Figure S1. Segmentation and reconstruction of the skull of *Eunotosaurus africanus*. Related to Figure 1. Segmentation, retrodeformed reconstruction, coloured line drawing, and line drawing with silhouette of *E. africanus* specimen CM-777, informed by all known specimens of *Eunotosaurus,* shown in (a,e,i,m) right lateral, (b,f,j,n) occipital, (c,g,k,o) dorsal, and (d,h,l,p) ventral views. Abbreviations: a, articular; an, angular; bo, basioccipital; d, dentary; ect, ectopterygoid; ep, epipterygoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pbs, parabasisphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pp,postparietal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; stp, stapes; tab, tabular; v, vomer. Scale bar, 1 cm.

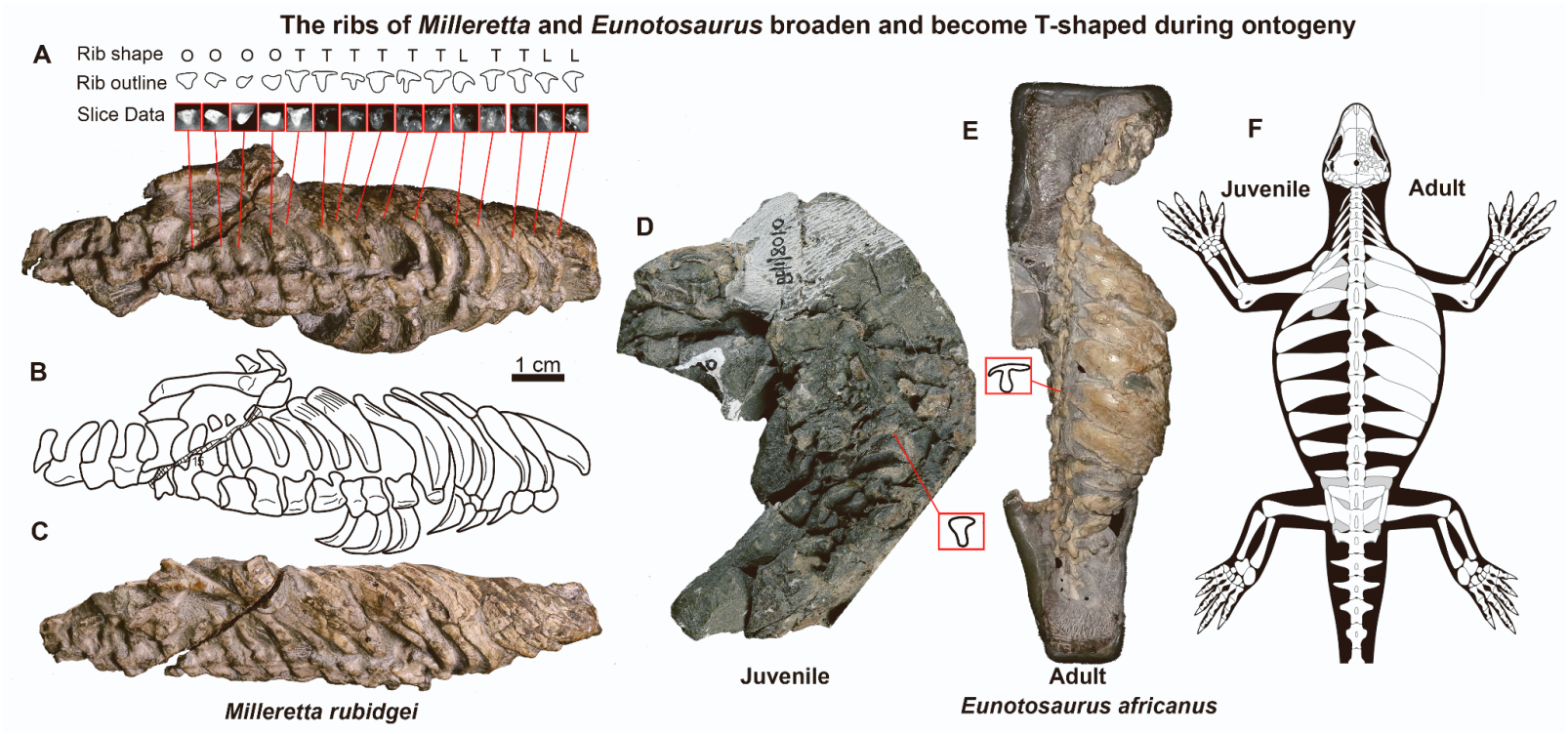

Figure S2. **Dorsal and left ventrolateral views of the postcranial anatomy of *Milleretta rubidgei* specimen BP/1/2040 compared with specimens of *Eunotosaurus*, showing the development of the dorsal ribs through ontogeny. Related to Figure 1.** (a) specimen and (b) corresponding line reconstruction in dorsal view, and (c) specimen in ventrolateral view. Cross-sections of the dorsal ribs closely resemble those of *Eunotosaurus africanus*; ribs are T-shaped throughout most of the trunk, becoming more L-shaped or rounded toward the sacral and cervical regions. (d) BP/1/8010, newly discovered juvenile of *E. africanus* with large gaps between succeeding dorsal ribs, (e) CM 86/341, adult of *E. africanus*, showing broadly overlapping dorsal ribs, and (f) line reconstruction of *E. africanus* in dorsal view summarizing juvenile and adult morphology. Reconstruction by Cy Marchant.

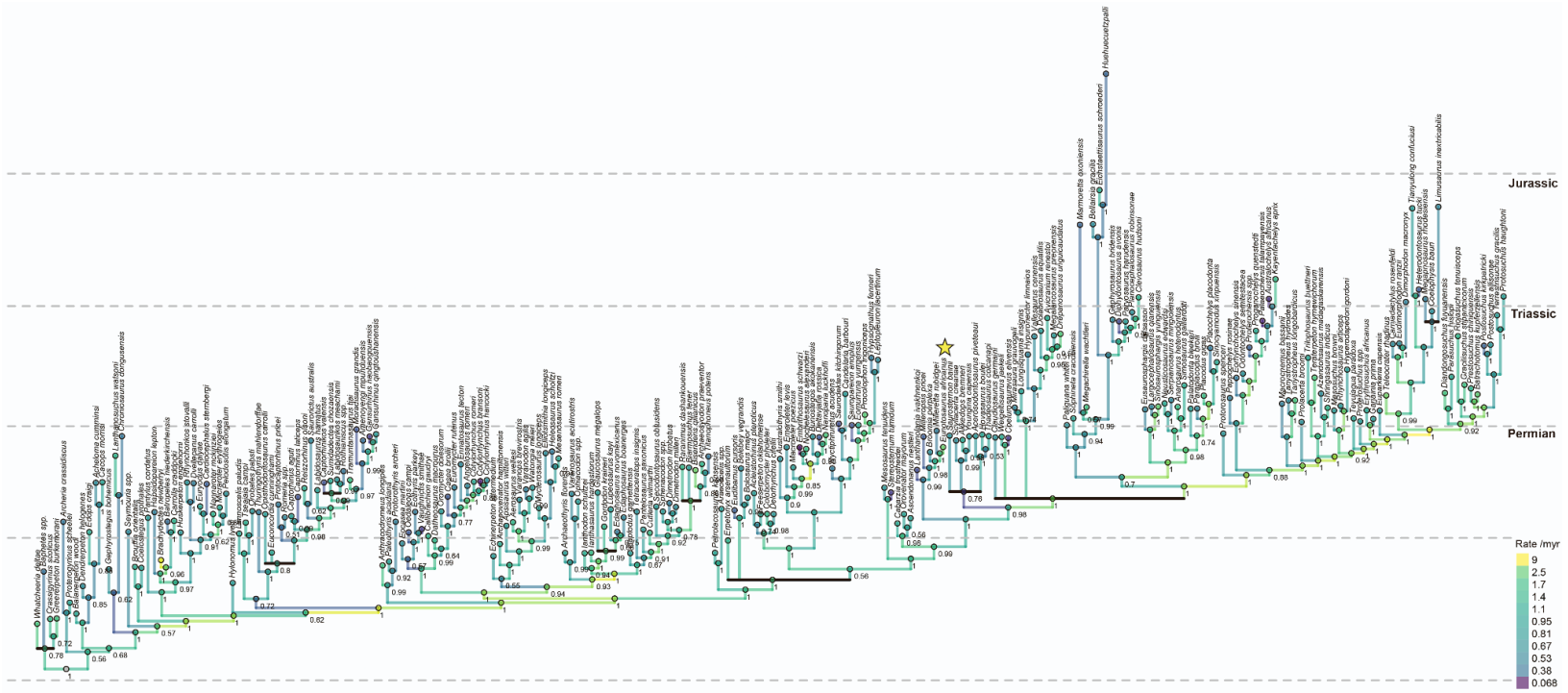

Figure S3. Majority-rule consensus tree from Bayesian phylogenetic analysis. Related to Figure 4. Majority-rule consensus topology recovered from Bayesian inference using a time-calibrated fossilized birth–death (FBD) model. Nodes with posterior probabilities <0.5 are collapsed. See OSF link for higher-resolution version of this image during review.

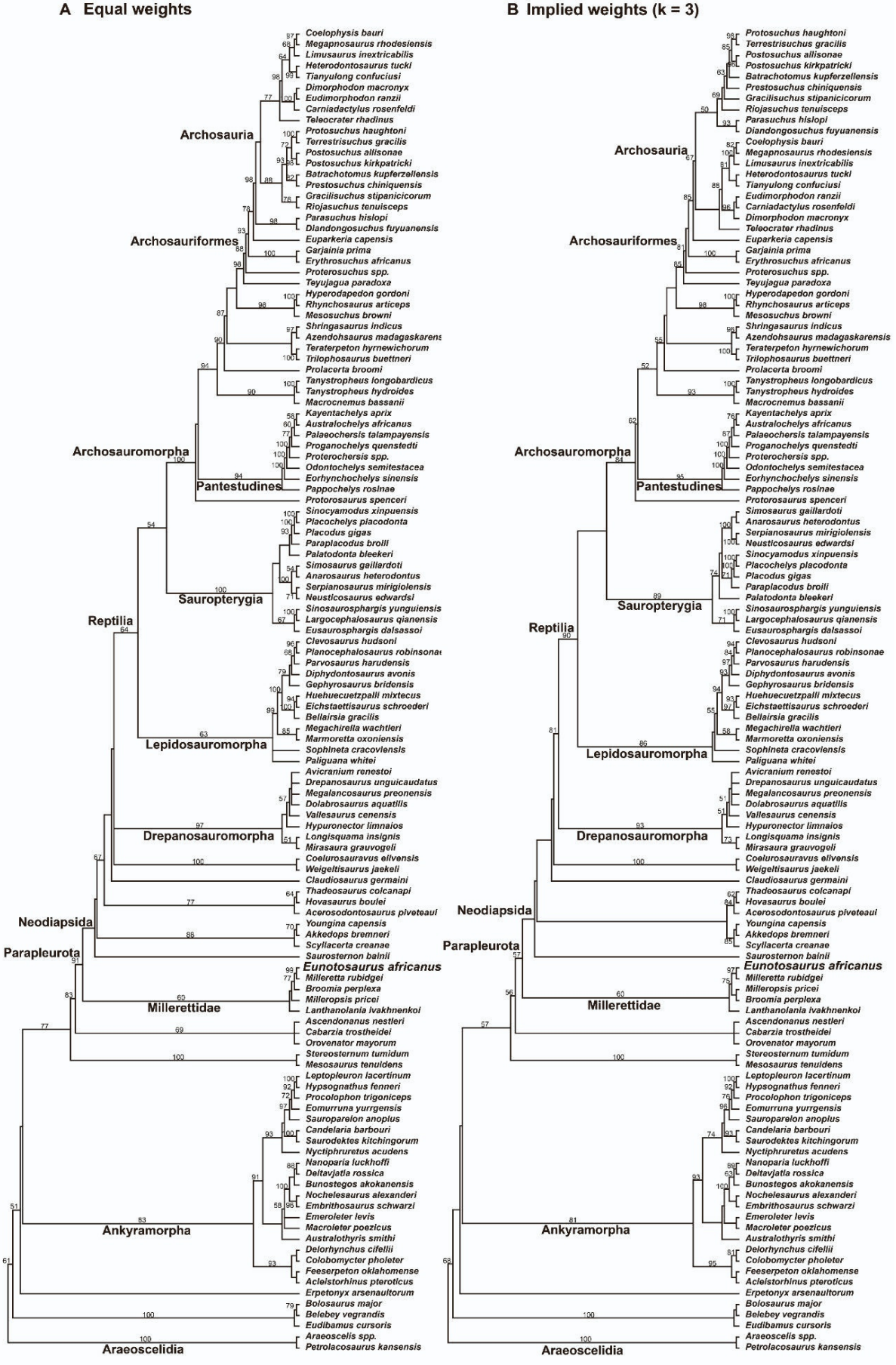
A Equal weights
B Implied weights (k = 3)
Archosauria
Archosauriformes
Archosauromorpha
Pantestudines
Sauropterygia
Reptilia
Lepidosauromorpha
Drepanosauromorpha
Neodiapsida
Parapleurota
Millerettidae
Ankyramorpha
Araeoscelidia
Coelophysis bauri
Megapnosaurus rhodesiensis
Limusaurus inextricabilis
Heterodontosaurus tucki
Tianyulong confuciusi
Dimorphodon macronyx
Eudimorphodon ranzii
Carniadactylus rosenfeldi
Teleocrater rhadinus
Protosuchus haughtoni
Terrestrisuchus gracilis
Postosuchus allisonae
Postosuchus kirkpatricki
Batrachotomus kupferzellensis
Prestosuchus chiniquensis
Gracilisuchus stipanicicorum
Riojasuchus tenuisceps
Parasuchus hislopi
Diandongosuchus fuyuanensis
Euparkeria capensis
Garjainia prima
Erythrosuchus africanus
Proterosuchus spp.
Teyujagua paradoxa
Hyperodapedon gordoni
Rhynchosaurus articeps
Mesosuchus browni
Shringasaurus indicus
Azendohsaurus madagaskarens
Teraterpeton hyrnewichorum
Trilophosaurus buettneri
Prolacerta broomi
Tanystropheus longobardicus
Tanystropheus hydroides
Macrocnemus bassanii
Kayentachelys aprix
Australochelys africanus
Palaeochersis talampayensis
Proganochelys quenstedti
Proterochersis spp.
Odontochelys semitestacea
Eorhynchochelys sinensis
Pappochelys rosinae
Protorosaurus spenceri
Sinocyamodus xinpuensis
Placochelys placodonta
Placodus gigas
Paraplacodus broili
Palatodonta bleekeri
Simosaurus gaillardoti
Anarosaurus heterodontus
Serpianosaurus mirigiolensis
Neusticosaurus edwardsi
Sinosaurosphargis yunguiensis
Largocephalosaurus qianensis
Eusaurosphargis dalsassoi
Clevosaurus hudsoni
Planocephalosaurus robinsonae
Parvosaurus harudensis
Diphydontosaurus avonis
Gephyrosaurus bridensis
Huehuecuetzpalli mixtecus
Eichstaettisaurus schroederi
Bellairsia gracilis
Megachirella wachtleri
Marmoretta oxoniensis
Sophineta cracovlensis
Paliguana whitei
Avicranium renestoi
Drepanosaurus unguicaudatus
Megalancosaurus preonensis
Dolabrosaurus aquatilis
Vallesaurus cenensis
Hypuronector limnaios
Longisquama insignis
Mirasaura grauvogeli
Coelurosauravus elivensis
Weigeltisaurus jaekeli
Claudiosaurus germaini
Thadeosaurus colcanapi
Hovasaurus boulei
Acerosodontosaurus piveteaui
Youngina capensis
Akkedops bremneri
Scyllacerta creanae
Saurosternon bainii
Eunotosaurus africanus
Milleretta rubidgei
Broomia perplexa
Milleropsis pricei
Lanthanolania ivakhnenkoi
Ascendonanus nestleri
Cabarzia trostheidei
Orovenator mayorum
Stereosternum tumidum
Mesosaurus tenuidens
Leptopleuron lacertinum
Hypsognathus fenneri
Procolophon trigoniceps
Eomurruna yurrgensis
Sauroparelon anoplus
Candelaria barbouri
Saurodektes kitchingorum
Nyctiphruretus acudens
Nanoparia luckhoffi
Deltavjatia rossica
Bunostegos akokanensis
Nochelesaurus alexanderi
Embrithosaurus schwarzi
Emeroleter levis
Macroleter poezicus
Australothyris smithi
Delorhynchus cifellii
Colobomycter pholeter
Feeserpeton oklahomense
Acleistorhinus pteroticus
Erpetonyx arsenaultorum
Bolosaurus major
Belebey vegrandis
Eudibamus cursoris
Araeoscelis spp.
Petrolacosaurus kansensis

Figure S4. Strict consensus trees generated from parsimony analyses. Related to Figure 4. (A) Strict consensus tree of the equal weights analysis (out of 96 most parsimonious trees of 8425 steps) and (B) strict consensus tree of the extended implied weights analysis (k = 3) (out of 3 best fitting trees, Fit =593.57405.) focusing on total-group reptile relationships, with other tetrapods removed for readability. Bootstrap GC frequencies >50% are listed above each node.

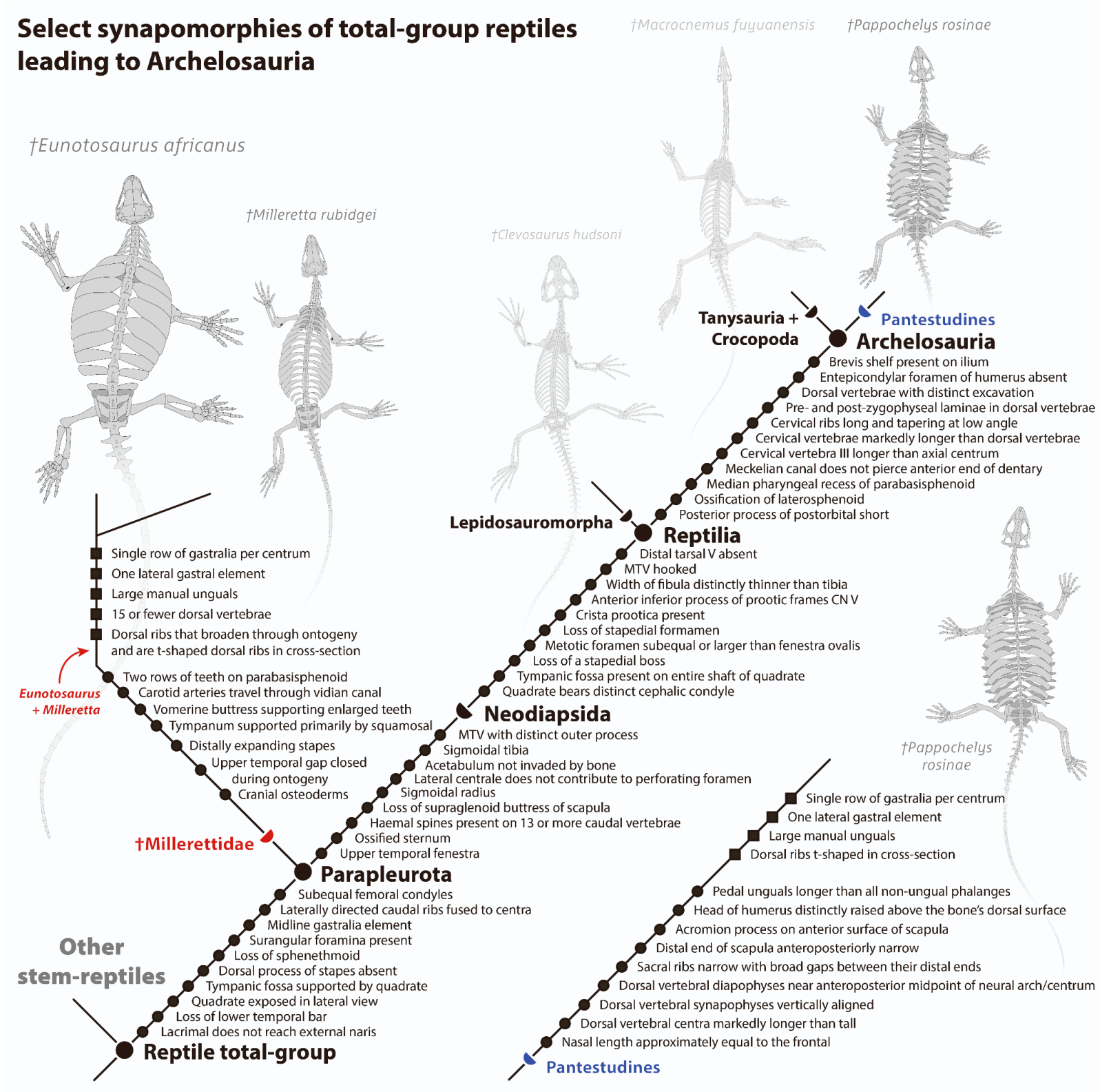
Select synapomorphies of total-group reptiles leading to Archelosauria
†Macrocnemus fuyuanensis
†Pappochelys rosinae
†Eunotosaurus africanus
†Milleretta rubidgei
†Clevosaurus hudsoni
Tanysauria + Crocopoda
Pantestudines
Archelosauria
Brevis shelf present on ilium
Entepicondylar foramen of humerus absent
Dorsal vertebrae with distinct excavation
Pre- and post-zygophyseal laminae in dorsal vertebrae
Cervical ribs long and tapering at low angle
Cervical vertebrae markedly longer than dorsal vertebrae
Cervical vertebra III longer than axial centrum
Meckelian canal does not pierce anterior end of dentary
Median pharyngeal recess of parabasisphenoid
Ossification of laterosphenoid
Posterior process of postorbital short
Lepidosauromorpha
Reptilia
Distal tarsal V absent
MTV hooked
Width of fibula distinctly thinner than tibia
Anterior inferior process of prootic frames CN V
Crista prootica present
Loss of stapedial formamen
Metotic foramen subequal or larger than fenestra ovalis
Loss of a stapedial boss
Tympanic fossa present on entire shaft of quadrate
Quadrate bears distinct cephalic condyle
Neodiapsida
MTV with distinct outer process
Sigmoidal tibia
Acetabulum not invaded by bone
Lateral centrale does not contribute to perforating foramen
Sigmoidal radius
Loss of supraglenoid buttress of scapula
Haemal spines present on 13 or more caudal vertebrae
Ossified sternum
Upper temporal fenestra
Parapleurota
Subequal femoral condyles
Laterally directed caudal ribs fused to centra
Midline gastralia element
Surangular foramina present
Loss of sphenethmoid
Dorsal process of stapes absent
Tympanic fossa supported by quadrate
Quadrate exposed in lateral view
Loss of lower temporal bar
Lacrimal does not reach external naris
Reptile total-group
Other stem-reptiles
Single row of gastralia per centrum
One lateral gastral element
Large manual unguals
15 or fewer dorsal vertebrae
Dorsal ribs that broaden through ontogeny and are t-shaped dorsal ribs in cross-section
Eunotosaurus + Milleretta
Two rows of teeth on parabasisphenoid
Carotid arteries travel through vidian canal
Vomerine buttress supporting enlarged teeth
Tympanum supported primarily by squamosal
Distally expanding stapes
Upper temporal gap closed during ontogeny
Cranial osteoderms
†Millerettidae
†Pappochelys rosinae
Single row of gastralia per centrum
One lateral gastral element
Large manual unguals
Dorsal ribs t-shaped in cross-section
Pedal unguals longer than all non-ungual phalanges
Head of humerus distinctly raised above the bone's dorsal surface
Acromion process on anterior surface of scapula
Distal end of scapula anteroposteriorly narrow
Sacral ribs narrow with broad gaps between their distal ends
Dorsal vertebral diapophyses near anteroposterior midpoint of neural arch/centrum
Dorsal vertebral synapophyses vertically aligned
Dorsal vertebral centra markedly longer than tall
Nasal length approximately equal to the frontal
Pantestudines

Figure S5. Permo-Triassic reptile relationships and key synapomorphies. Related to Figure 4. Diagram of Permo-Triassic reptile relationships focusing on synapomorphies of nodes leading to Millerettidae and Pantestudines. All reconstructions by Cy Marchant and LiterallyMiguel.

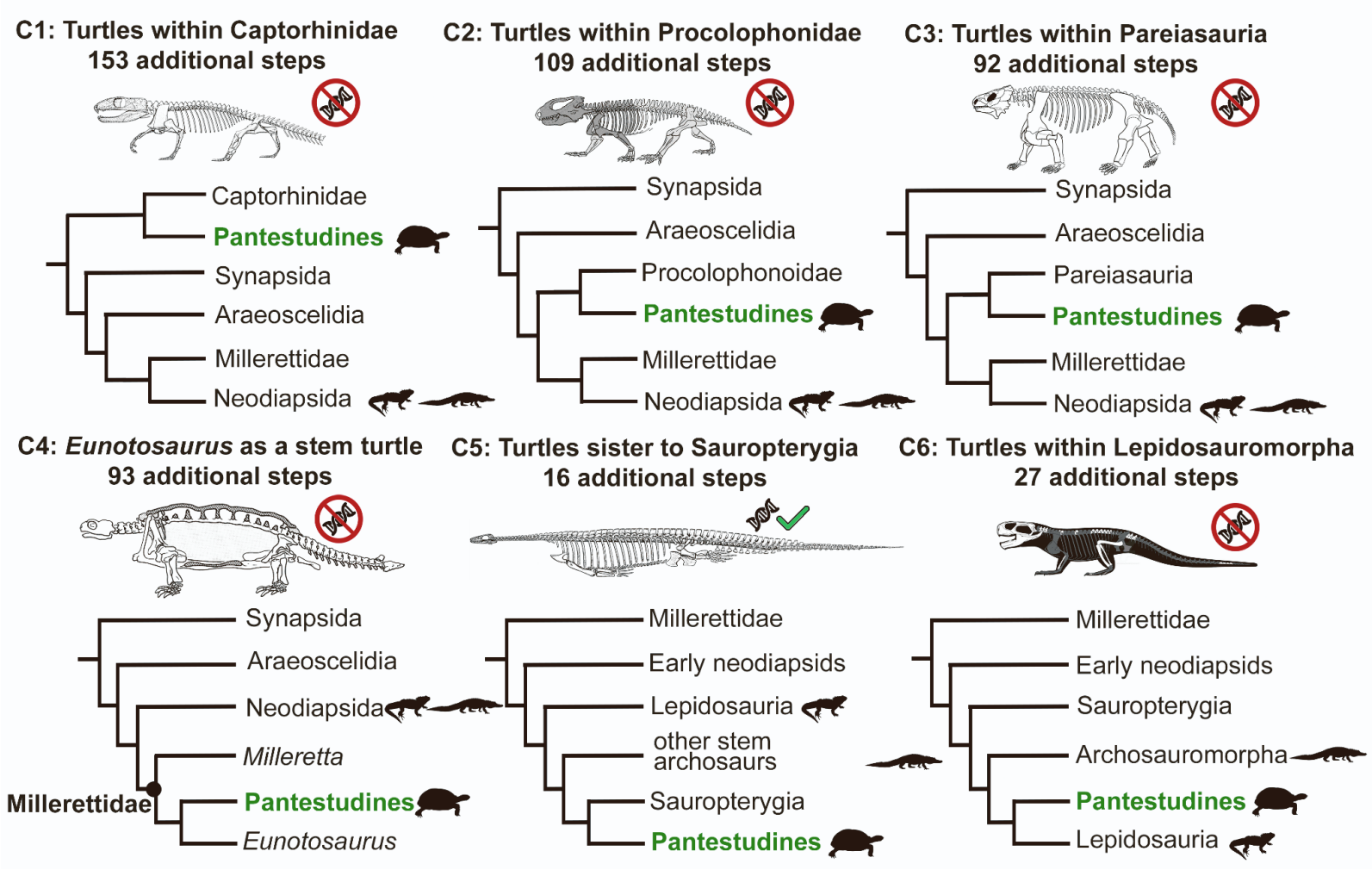

Figure S6. Constraint analyses evaluating alternative hypotheses for the origin of turtles. Related to STAR methods. Simplified strict-consensus topologies recovered from maximum parsimony analyses under competing phylogenetic constraints. Trees show the additional steps required to constrain Pantestudines within (C1) Captorhinidae (+153 steps, p <0.0001*, reconstruction from Heaton and Reisz 1980), (C2) Procolophonoidea (+109 steps, 109 p <0.0001*, reconstruction from Zaher et al. 2019), and (C3) Pareiasauria (+92 steps, p <0.0001*, reconstruction from Tsuji 2013), as well as (C4) forcing *Eunotosaurus africanus* as a stem turtle (+93 steps, p <0.0001*, reconstruction from Gaffney 1990). Additional analyses include placement of turtles as sister to Sauropterygia (C5; +16 steps, reconstruction from Carroll and Gaskill 1985) and within Lepidosauromorpha (C6; +27 steps, p = .0046). Of these constrained hypotheses, only the sister-group relationship between turtles and Sauropterygia (C5, p = .1315, reconstruction by Maurissauro) cannot be statistically rejected. Green check mark denotes congruence with molecular hypotheses of turtle origins within Archosauromorpha.

Taxon	Tree Length	Add. Steps	P-value	MPT's
Turtles among Captorhinidae	8398	153	<0.0001*	480
Turtles as procolophonids	8354	109	<0.0001*	196
Turtles among Pareiasauria	8337	92	<0.0001*	274
Eunotosaurus as a stem turtle	8338	93	<0.0001*	292
Turtles as sister to Sauropterygia	8261	16	.1315	384
Pantestudines within Lepidosauromorpha	8272	27	.0046*	292

Table S1. Results for Constraint Analyses and Templeton Tests. Related to STAR Methods. Constrained topologies of amniote relationships testing alternative hypotheses of turtle origins, where MPT= the number of most parsimonious trees for the constrained topology. Add. Steps= number of steps in addition to the optimal MPT's, and P-value=probability value of constraint MPTs.